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Individual variability in diel vertical migration of a marine copepod: Why some individuals remain at depth when others migrate

Abstract—The diel vertical migration (DVM) of the copepod *Metridia pacifica* was examined in Dabob Bay (47°45.05'N, 122°49.71'W), a fjord in Washington state. Although the population showed deep daytime residence (75–175 m), a proportion of the population was found in the surface waters at night. For individuals that migrated to the surface, the mean size of the oil sac was much smaller than those that remained at depth (mean lengths of oil sac 0.25 mm for individuals collected between 0 and 25 m at night, compared with 0.43 mm for individuals from between 125 and 175 m). Similarly, the C:N ratio was lower for animals collected from near the surface, indicative of their lower lipid reserves. These results suggest that individual variability in DVM was influenced by body condition, with those animals with larger lipid stores not needing to risk coming to the surface to feed at night.

The ubiquity of diel vertical migration (DVM) in planktonic systems has led to extensive investigations into this phenomenon over the last century and more. Although early studies focused on quantifying the occurrence of this behavior in different taxa, over recent decades there has been increased consideration of the ultimate factors that drive this behavior (e.g., Zaret and Suffern 1976; Dagg et al. 1998), the proximate cues that regulate the timing of vertical movements (e.g., Ringelberg 1999), and the biogeochemical implications in terms of the vertical transport of elements such as carbon and nitrogen (e.g., Longhurst and Harrison 1989).

The normal pattern for DVM is for animals to ascend from depth around dusk, feed near the surface during the night, descend around dawn, and then fast at depth during the day. The generally accepted cost of these daily vertical movements is that individuals at depth during the day are separated from their near-surface phytoplankton and microzooplankton prey and so have a reduced feeding rate. This general scenario is supported by gut analysis, although occasionally material is found in the guts of migrants during the day, which may reflect that some feeding continues at depth (e.g., Dagg et al. 1998).

There is now very extensive evidence that the ultimate function of normal DVM is to reduce the risk of predation from visual predators such as fish, the so-called predator-evasion hypothesis (Zaret and Suffern 1976). For example, DVM tends to be most pronounced in larger and/or more highly pigmented species, i.e., those that are more susceptible to visual predation because of their greater visibility (Hays 1995 and references therein); within species, DVM is more pronounced when planktivorous fish are more abun-

dant (Bollens and Frost 1989); and in artificial enclosures, DVM can readily be induced by the addition of planktivorous fish (Dawidowicz et al. 1990). Similarly, when normally migrating invertebrate predators are abundant, their prey may exhibit reverse DVM (populations near the surface during the day and deeper at night), again in order to reduce their risk of predation (e.g., Neill 1990). However, although the evidence in support of the predator evasion hypothesis is very strong, questions remain about the factors that drive individual variability in vertical movements. For example, although there may be general upward and downward movements at dawn and dusk, respectively, only a proportion of individuals may migrate on this schedule, with some of the population remaining at depth in all parts of the diel cycle (e.g., Bollens and Frost 1989, 1991; Dagg et al. 1998). There is little empirical evidence to explain what drives such individual variability. However, given the conceptual framework provided by the predator-evasion hypothesis, we can develop testable a priori predictions about potential causal factors.

The predator-evasion hypothesis explains DVM behavior on the basis of the lower ambient light levels near the surface at night, which make it harder for visual predators to perceive their prey. However, because the size of animals also influences their visibility, it might be predicted that smaller individuals may be more likely to come to the surface and will spend longer at the surface than larger individuals. Comparison between species and developmental stages support this argument. For example, juvenile stages of the copepod *Metridia lucens* spend longer near the surface than adult stages (which are larger), whereas the larger copepod, *Metridia longa*, spends even less time at the surface each night (Hays 1995). Similarly, De Robertis et al. (2000) have recently shown this same link between the size of individuals and their residency at the surface. These same arguments for the importance of size may similarly apply within the same developmental stage for a single species—i.e., when planktivorous fish are abundant, larger individuals may not migrate to the surface because of their higher risk of predation. Because there is a cost to near-surface residence in terms of the increased risk of predation, the predator-evasion hypothesis predicts that individuals would only incur this cost when it is outweighed by the benefit of near-surface foraging. Theoretical arguments suggest that the benefit of migrating to the surface may be dependent on the body condition of individuals (Fiksen and Carlotti 1998; Sekino and Yamamura 1999): for example, for animals with large lipid reserves, there may be less benefit to near-surface foraging, and so

these individuals may remain at depth until reserves are depleted to some threshold level that initiates migration.

In short, we might expect individual variability in vertical migration to be linked to the size and/or body condition of individuals. We therefore set out to measure the size and body condition of individuals at different depths over the diel cycle within a population of marine copepods in which only a proportion of individuals migrated to the surface each night.

Materials and methods—Sampling took place on 11–13 September 1998 at a fixed site in Dabob Bay (47°45.05'N, 122°49.71'W), a fjord in Washington state. Water depth was 190 m. A vertically deployed opening/closing Puget Sound net (mouth diameter 1 m, mesh size 571 μm) was used to sample four discrete depth strata: 0–25, 25–75, 75–125, and 125–175 m; from these samples, we examined the abundance, body size, gut fullness, oil sac size, and carbon and nitrogen content of adult female *M. pacifica*, a well-known vertical migrant in this area.

Around midnight on the nights of 11 and 12 September and around midday on 12 September, we made a series of net deployments to examine the day/night vertical distribution. These samples were preserved in buffered formalin for subsequent analysis. In the laboratory, the samples were equally split into aliquots that represented 2% of the total catch, and then all the animals in five aliquots were counted (i.e., 10% of the entire sample was counted). Levels of abundance in the different depth strata were then quantified in terms of numbers per m^3 under the assumption of 100% filtration efficiency of the net, which is a valid assumption given the coarse mesh size and short tows. We measured the prosome length of between 10 and 20 randomly selected animals from each haul and, from the midnight samples, the length of the oil sac and the gut fullness (a visual estimate of the proportion of the gut that contained material) for 10 individuals per haul.

In addition, we made net deployments at other times of the night (18:30–05:30) to collect animals for CN analyses. Individuals for CN analysis were placed into ultraclean tin capsules (Elemental Microanalysis Ltd.) (generally 10 individuals per capsule, to provide sufficient material) and then frozen. These samples were dried at the University of Washington before transport to University of Wales, Bangor, where particular organic carbon/particulate organic nitrogen concentrations were determined with a Europa Scientific CN analyser, with use of acetanilide as a standard.

Results—The midnight/midday vertical series showed that part of the population were exhibiting DVM. During the day, *M. pacifica* were found almost exclusively below 75 m, with approximately equal abundance between 75–125 and 125–175 m. At night, the abundance of animals in the deepest strata (125–175 m) changed little, which suggests that these animals were nonmigratory, but between 75 and 125 m the abundance declined markedly in line with increased abundance in the two shallowest depth strata (0–25 and 25–75 m) (Fig. 1).

Animals collected in the two shallowest depth strata at night had material in their guts that indicated that they had

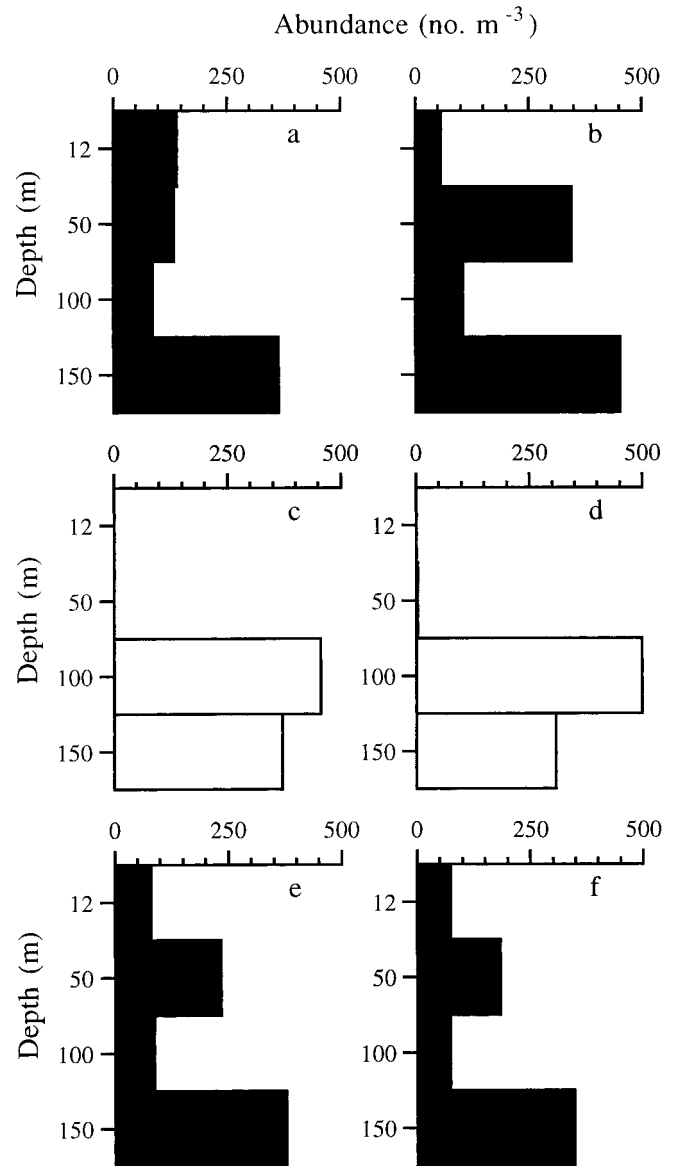


Fig. 1. The day/night abundance of *M. pacifica* at different depths. Bars show the midpoint of each of the four sampled depth strata. (a, b) Profiles around midnight on 11 September. (c, d) Profiles around midday on 12 September. (e, f) Profiles around midnight on 12 September.

fed recently, whereas those deeper had almost completely empty guts (Fig. 2a). Differently sized animals occurred at different depths. For example, in the midnight vertical series, the mean size of animals was 1.63 mm between 0 and 25 m and increased to 1.68 mm between 125 and 175 m. In absolute terms, however, this difference in size is very small (3%) (Fig. 2b). In contrast, there were much larger differences in the size of the oil sac from individuals collected at different depths, with the mean oil sac length increasing from 0.25 mm between 0 and 25 m up to 0.43 mm between 125 and 175 m, a 72% increase (Fig. 2c). The C:N ratio of animals also increased with depth (Fig. 2d) from a mean value of 5.98 between 0 and 25 m to a mean value of 7.25

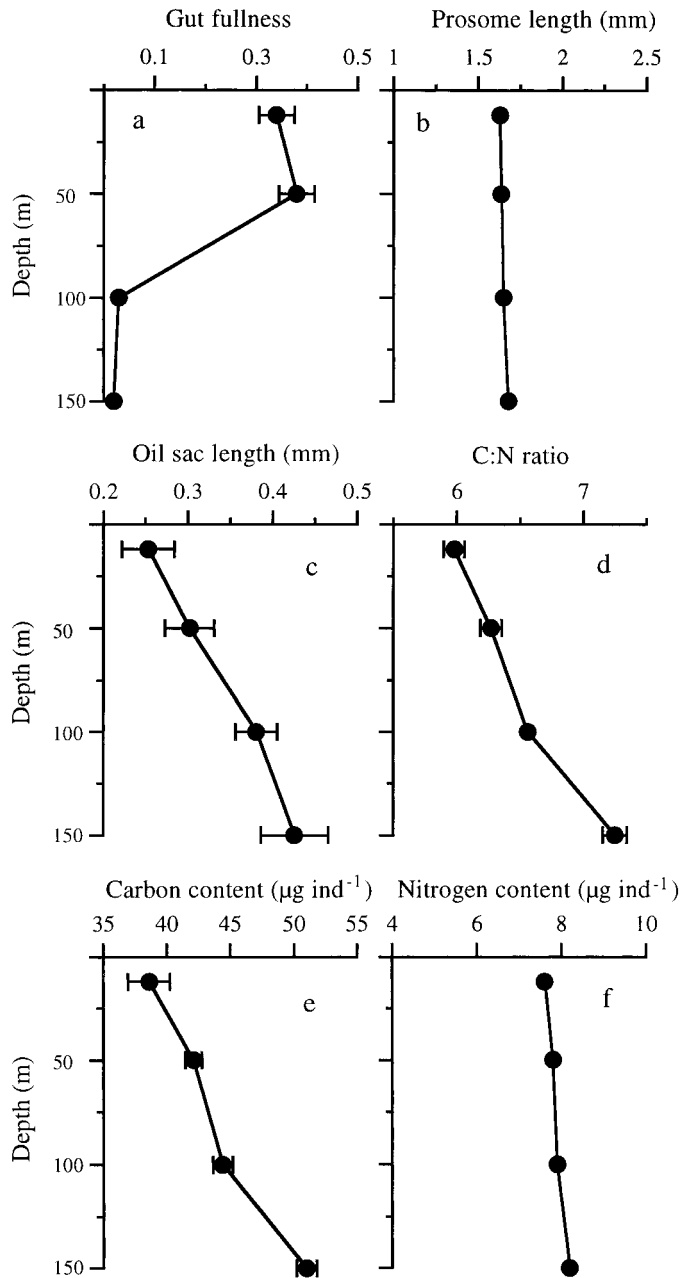


Fig. 2. For *M. pacifica* collected at night from different depths, (a) the mean gut fullness, (b) the mean prosome length, (c) the mean oil sac length, (d) the mean C:N ratio, (e) the mean C content per individual, and (f) the mean N content per individual. All error bars are ± 1 SE and are smaller than the plot symbol if not shown. The mean prosome length of individuals collected around midday lay within the same plot symbols as those shown and so are omitted for clarity. The x axes for prosome length and oil sac length are scaled to cover the same relative range, to facilitate visual comparison in the variation with depth for these two parameters.

between 125 and 175 m (Fig. 2d). This increase reflected the fact that the C content of individuals increased markedly with depth (from a mean of $38 \mu\text{g C ind}^{-1}$ between 0 and 25 m up to $51 \mu\text{g C ind}^{-1}$ between 125 and 175 m) compared with their nitrogen content (Fig. 2e,f).

Discussion—It is well known that the body condition of animals may have major impacts on their behavior under a wide range of circumstances. For example, there may be a threshold level of energy reserves that is required to initiate breeding in some reptiles (e.g., Naulleau and Bonnet 1996), whereas in other groups energy reserves may dictate patterns of foraging. For example, although most microchiropteran bats are nocturnal, emerging to hunt for insects at night, daytime flying is occasionally reported and has been linked to poor foraging conditions over previous nights, a consequent energy shortfall, and hence the need for individuals to emerge and feed during the day, even though this increases their risk of predation from raptorial birds (Speakman 1991). This example is mentioned because exactly the same ecological constraints may apply to zooplankton: when food is scarce, individuals may remain continuously at the surface rather than descending at dawn, because they are unable to feed to satiation within the hours of darkness (Huntley and Brooks 1982).

Given the widespread importance of body condition throughout the animal kingdom, it is not surprising that some aspects of the life history of zooplankton are closely coupled to their condition. For example, in the euphausiid *Megan-yctiphanes norvegica*, Tarling et al. (1999) have shown that individuals descend and remain at depth while moulting, presumably in order to reduce their risk of predation when they lack a hard exoskeleton and hence are more vulnerable. Similarly, Bollens and Frost (1991) have shown that the DVM behavior of female *Euchaeta elongata* is influenced by whether they are ovigerous or not, with egg-carrying females remaining at depth, again because of their higher risk of predation. However, it is surprising that the impact of body condition on DVM behavior has not been more extensively explored. Recently, theoretical arguments have been presented that implicate the importance of body condition, with the prediction that animals that have greater energy reserves will be less inclined to run the risk of coming to surface (Sekino and Yamamura 1999). However, this prediction has been tested with little empirical evidence.

Although there are problems with interpreting the movements of individuals through the use of net samples, because individuals may behave differently from the population as a whole (Pearre 1979), the pattern of DVM that we recorded is essentially the same as that recorded previously in Dabob Bay and elsewhere in the world's oceans and lakes, in that only a proportion of the population seemed to migrate to the surface waters at night. One of the axioms of the predator-evasion hypothesis is that there is a cost of residence at depth in terms of reduced feeding. However, quantitative assessment of the level of feeding of zooplankton in natural conditions is problematic. The most widely used technique has been the analysis of gut fluorescence, although this approach is hampered by the fact that it does not measure nonphytoplankton prey and also may become only semiquantitative because of the destruction of fluorescent pigments during digestion (e.g., McLeroy-Etheridge and McManus 1999). Although our simple approach of visually assessing the fullness of the gut is similarly likely to be only semiquantitative, it clearly showed that animals near the surface at night had material in their guts, whereas those at depth did not. Thus,

in our study, as in those reported elsewhere, there was strong evidence for a cost to deep residence. The counterbalancing benefit is likely to be reduced predation from planktivorous fish, and certainly in the fjords of Washington such fish may be abundant (e.g., Bollens and Frost 1989). What then were the reasons why some individuals remained at depth during the night, whereas others were found near the surface?

Size clearly plays a role in determining interspecific and ontogenetic patterns of DVM (e.g., Hays 1995). However, the difference in size between individuals near the surface and those at depth was very small in absolute terms (3%), and it is hard to envisage that this small difference could produce massive differences in the risk of predation at the surface. Far more startling was the individual variability in the size of the oil sac. In essence, animals collected near the surface at night tended to have a relatively small oil sac compared with animals collected at greater depths. The large oil sac of deep animals is probably not a consequence of their depth of occurrence, given that the lack of feeding at depth would be expected to lead to reduced energy reserves of this group. Rather, these animals must almost certainly have assumed their deep residence after building up their energy reserves by near-surface feeding.

The oil sac of calanoid copepods is a site of major energy storage, and, although the amount of stored lipid (and the different lipid classes) can be assessed by biochemical techniques, it has been shown that simple linear measurements of the size of the oil sac gives a very good measure of the overall lipid reserves (Miller et al. 1998). Consequently, the use of simple linear measurements of oil sac size has been strongly advocated (Reiss et al. 1999). Our results therefore show that nonmigrants that remained at depth had relatively large energy reserves. This conclusion is reinforced by the increase in the C:N ratio with increasing depth. Because lipid has little N and protein is N rich, a higher C:N ratio indicates that a greater proportion of the body is composed of lipid (e.g., Irigoien et al. 1998)—i.e., their higher C:N ratio reiterates that animals collected in the deepest strata at night had the greatest proportion of lipid.

For some calanoid copepods, such as *Calanus finmarchicus*, there is seasonal dormancy, with individuals overwintering at great depth for many months, during which they survive on lipid reserves (Hirche 1996). It is not known whether oil sac size influences the visibility of copepods to fish in such cases. For *C. finmarchicus*, depth seems to covary with body condition, with the C5 individuals that occur at greater depth having increased lipid reserves (e.g., Jónasdóttir 1999). Thus, body condition seems to have important implications for whether *C. finmarchicus* enters deep-water diapause. In contrast to *C. finmarchicus*, a strong pattern of seasonal diapause seems less pronounced for *M. pacifica*. For example, Osgood and Frost (1994) concluded that this species shows no seasonal diapause in Dabob Bay, with reproduction continuing, at least to some extent, throughout the year; a similar conclusion was reached by Ohman et al. (1998) for this species in southern California. By maintaining animals from the deep strata in filtered seawater and then monitoring their change in condition, it would be possible to directly quantify the expected duration (e.g., days or weeks) of their nonmigratory behavior, i.e.,

how long it would take before their body condition fell below a threshold level to initiate DVM. In the absence of these experiments, we can make a more “rough-and-ready” calculation for how long their extra lipid reserves might sustain the animals resident at depth. The metabolic rates reported for adult female *M. pacifica* have been reviewed by Batchelder (1986), with minimal and maximal values of 1.5 and 4.5 $\mu\text{g C ind}^{-1} \text{ day}^{-1}$, respectively. If we assume that the increased carbon content (51 vs. 38 $\mu\text{g C ind}^{-1}$) of the deep versus shallow individuals is all lipid, then this range of reported metabolic rates would mean that the extra 13 $\mu\text{g C ind}^{-1}$ would sustain these deep animals for between 3 and 9 d. This is clearly only a crude estimate, but nevertheless these calculations are probably sufficiently robust for us to be fairly confident that the extra lipid reserves of the animals at depth would sustain them for days rather than months, consistent with previous conclusions that *M. pacifica* does not enter long-term diapause. Rather, we would predict that in a matter of days the resident deep animals would have depleted their energy reserves to such a level that ascent to the surface at night to feed would be initiated. Our results therefore lend empirical support to theoretical models that predict that DVM behavior will change for individuals as their body condition oscillates, with continuous deep residence when lipid reserves are high and then DVM with nighttime feeding when lipid reserves have dropped (Sekino and Yamamura 1999).

In conclusion, our results suggest that there was a major difference in the body condition between migrants and nonmigrants. In essence, it would appear that animals with high lipid stores were able to remain at depth, because they did not risk imminent starvation, so there was no need to run the increased risk of predation near the surface.

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Daphnia food limitation in three hypereutrophic Dutch lakes: Evidence for exclusion of large-bodied species by interfering filaments of cyanobacteria

Abstract—The Loosdrecht Lakes comprise three shallow, hypereutrophic lakes in The Netherlands. Research conducted over the past two decades suggests that absence of large-bodied *Daphnia* from these lakes can be explained by size-specific effects of both poor food quality and predatory mortality. The phytoplankton is dominated by filamentous cyanobacteria, which interfere with the feeding of large-bodied *Daphnia*. Moreover, dense populations of planktivorous fish are expected to feed selectively on larger prey. More recent research, however, suggests that the growth of the small native *Daphnia* species, *Daphnia cucullata*, is limited by low dietary phosphorus (P). In this study, we compared the growth and feeding rates of four *Daphnia* taxa representing a gradient in body size. In each of 10 growth experiments, native *D. cucullata*

feeding in natural seston exhibited improved growth in response to additions of phosphate and the P-rich cyanobacterium *Synechococcus*. The two largest species, *Daphnia magna* and *Daphnia galeata*, however, failed to grow in natural seston, even when the seston was supplemented with phosphate, *Synechococcus*, or *Scenedesmus*. A *D. galeata* × *cucullata* hybrid exhibited weak growth in natural seston and no response to the supplements. Feeding experiments with polystyrene beads show that feeding inhibition in natural seston increased markedly with increased *Daphnia* size. Our results verify that *Daphnia* differing in size face different food quality constraints. The growth of native *D. cucullata* (adult size 0.6–0.8 mm) is reduced by P deficiency, whereas larger *Daphnia* appear to be excluded by interfering filaments of cyanobacteria.